A NORTH BORNEAN PYGMY SQUIRREL, *GLYPHOTES SIMUS* THOMAS, AND ITS RELATIONSHIPS

By J. E. HILL

Only three specimens of this unusual Pygmy Squirrel, *Glyphotes simus*, have been recorded since publication of the description in 1898. It has received little attention in the literature, no doubt through the paucity of the available material, and has remained little known. The British Museum (Natural History) has recently received a specimen of *Glyphotes* from the Institute for Medical Research, Kuala Lumpur, and this accession has prompted further examination of the genus.

I am indebted to J. L. Harrison, lately of the Institute for Medical Research, who arranged the gift of *Glyphotes*; to C. A. Gibson-Hill, Director, Raffles Museum, Singapore and to Tom Harrisson, Curator, Sarawak Museum, Kuching, who courteously loaned the material of *Glyphotes* in their care for comparison; lastly, to R. W. Hayman, of the British Museum (Natural History), for his valuable advice and criticism during the preparation of this paper.

Apart from the original description, incidental mention in faunal works such as that of Banks (1931) and enumerations of the principal characters such as that of Ellerman (1940), previous published work on the genus appears limited to that of Chasen & Kloss (1927). Their paper gives a brief account of the known specimens at that date, with measurements, and records an additional specimen.

The following account is based on five specimens of *Glyphotes simus*, which so far as I have been able to ascertain represent the total preserved in collections at the present time. They are:

(i) British Museum 98.11.3.6. The type specimen. Adult, sex unknown. Collected on Mount Kina Balu, North Borneo, by A. Everett. Skin and skull, the rear of the cranium missing.

(ii) Sarawak Museum 55.11. Adult male. Collected on Mount Merapok (Mount Marabok), Brunei, by J. Waterstraat in December, 1899. Skin and skull, the latter not available: the Sarawak Museum collection was disorganized during the Japanese Occupation, 1941–45. Formerly British Museum 0.10.8.2 but given in exchange to the Sarawak Museum in 1901. As remarked by Chasen & Kloss (1927) the label has been marked "Co-type of the species". However, as these authors point out, the specimen was collected in the year following publication of the description and no mention is made by Thomas of any specimen other than the type.

(iii) Sarawak Museum 55.12. Adult female. Collected on Mount Kina Balu, North Borneo at 3,500 ft. by a native collector on 10th September, 1913. Skin

and skull: the latter not available (see (ii)). Formerly referred to *Callosciurus notatus*, which possibly explains why it was overlooked by Chasen & Kloss (1927).

(iv) Raffles Museum. Subadult female. Collected at Tenompok, Kota Bellud, near the south foot of Mount Kina Balu, North Borneo, by a native collector on 10th June, 1925. Skin and skull, the latter much broken and fragmentary.

(v) British Museum 58.446. Adult male. Collected at Tenompok, Mount Kina Balu, North Borneo, by a collector of the Institute for Medical Research, Kuala Lumpur, on 16th June, 1952. Specimen preserved in alcohol, the skull and baculum extracted and cleaned.

GLYPHOTES Thomas

1898 *Glyphotes* Thomas, *Ann. Mag. nat. Hist.* **2**: 250.

A genus of dwarf squirrel characterized by its short, broad rostrum, much reduced postorbital processes and peculiar, specialized incisors. The zygomatic plate slants upwards and is more nearly vertical than in *Callosciurus*. The lower jaw is weak, with low coronoid processes and slender, elongated condylar processes. The upper incisors are very broad and yet not thickened antero-posteriorly, their tips divergent from each other. The lower incisors are similar but are more strongly divergent. Cheek teeth 5/4, with their pattern as in *Callosciurus*.

Glyphotes simus Thomas

1898 *Glyphotes simus* Thomas, *Ann. Mag. nat. Hist.* **2**: 250. Mount Kina Balu, North Borneo.

Externally characterized by its deep, broad, short muzzle. A specimen in alcohol confirms the "stumpy-nosed" description applied by Thomas and indicates more than do study skins the depth of the muzzle in relation to its length. The ear is of the Callosciurine type and when laid forward reaches almost to the posterior canthus of the eye. The feet are of the normal tree squirrel pattern: of the four digits of the manus, D4 is slightly longer than D3 while the outer digits are equal in length and are about half the length of D4. The hallux is the shortest digit of the tarsus while D5 is considerably longer, nearly as long as D4, which only slightly exceeds in length D2 and D3. The claws are well developed, white tipped and dark brown at the base. The tail is rather narrow and is shorter than the head and body. External measurements (in millimetres) of B.M. 58.446: head and body 115, tail 95, hindfoot 27, ear 13.

The dorsum is dull grey, grizzled and flecked with pale buff. The dorsal pelage is typically of Callosciurine type, the short hairs of the underfur slate grey at the base and tipped with pale buff or straw colour. The longer, overlaying bristle hairs are black or chestnut based and are tipped with chestnut, with a subapical annulation of buff: not infrequently bristle hairs are found with dark tips and bases but with two annulations of buff separated by a central band of black. Occasionally, these hairs are black throughout their length. Essentially similar, but slightly shorter pelage extends over the nape and crown. The outer surfaces

of the legs and the dorsal surfaces of the fore feet are the same colour as the back while the dorsal surfaces of the hind feet are slightly more buffy. The bases of the claws are furnished with a small tuft of brighter, more buffy hairs. The sides of the muzzle are brighter buff than the back and there is an orange buff eye ring. The ears, especially on their posterior edge, are fringed with bright orange buff. There is a very indistinct postauricular patch of white. The white lateral flank stripes are broad and are usually the same width throughout their length : in the type specimen they are broader anteriorly than posteriorly. The black sublateral stripes are narrower and less prominent, more diffuse, especially posteriorly, where a suffusion of black tends to spread across the belly. The anterior part of the ventrum is dull orange buff : posteriorly the ventrum is buffy but is suffused with grey and overlaid slightly with black. The tail is blackish, grizzled with bright orange buff. The hairs are dark tipped and dark based with a broad sub-basal annulation of bright buff, sometimes with a second subterminal annulation of paler buff separated from the sub-basal annulation by a band of black.

The specimen from Mount Merapok, Brunei, is brighter and less greyish dorsally than those from Kina Balu. Its tail hairs are annulated with brighter orange and the underparts are more buffy and less suffused with grey, while the dorsal surfaces of the feet are warmer in tone. This circumstance was noted by Chasen & Kloss (1927), who compared this specimen with that listed as (iv) above.

Externally, *Glyphotes simus* is similar to *Callosciurus notatus dulitensis*, from which it may be distinguished by smaller size, foreshortened muzzle, paler underparts and feet, broader, more prominent white lateral stripes, less prominent black sublateral stripes, greyer back and darker tail. Dorsally, it is similar in colour to *Callosciurus nigrovittatus orestes* but is paler and less buff. The annulations of the tail hairs are brighter than in *orestes* while the underparts are predominantly buff and not grey.

The baculum of *Glyphotes simus* (Plates 8 (*c*)–8 (*f*)) is of the Callosciurine pattern, as described by Thomas (1915) and figured by Didier (1952). It consists of two parts, a slender, tapering shaft and a separate plate or lamina attached to its dorsal surface.[1] The shaft, which at its base and for most of its length is greater in depth than in width, is comparatively broad based and tapers only slightly in its proximal half, but beyond its centre point tapers more abruptly to a blunt point furnished laterally with two small barbs. Viewed laterally, the ventral face forms a compound curve, the proximal half concave, the distal half convex. The dorsal surface is concave, more especially in its distal portion, whereon is attached the separate lamina. Viewed dorsally, the baculum is a slender, straight shaft. The lamina originates from a point just posterior to the tip of the shaft and extends along the dorsal surface for about half the length of the shaft. It is parallel-sided for most of its length but for its posterior quarter tapers to a point and is free from attachment to the shaft. Anteriorly, it is bluntly pointed. Measurements of the baculum (in millimetres) : length of shaft 13·2 and length of lamina, 6·6.

[1] The surfaces of the baculum are described here according to the usage of Pocock (1923). The lamina is attached to that part of the shaft which in the extended penis is nearest to the belly, i.e. its upper or dorsal surface. The baculum, however, occurs in the distal portion of the penis which in the unextended condition is recurved to point posteriorly beneath the proximal portion of the penis. In this condition the lamina is ventrally placed in relation to the shaft.

It has been possible to examine the bacula of specimens representative of the following species of *Callosciurus*: *finlaysoni*, *erythraeus*, *flavimanus*, *notatus* and *prevosti*. Of these, the first three have the lamina attached to the central part of the shaft and not extending to the tip. The lamina is pointed anteriorly, is widest at a point some three-quarters of its length from the tip and tapers to a posterior point. The tip of the shaft is furnished with two lateral barbs and with a third, usually larger, dorsal barb. This structure is illustrated by Didier (1952). The bacula of *Callosciurus notatus* and *Callosciurus prevosti*, however, resemble that of *Glyphotes simus* in having the lamina, which is the same shape as in the preceding species, inserted immediately posterior to the tip of the shaft. Among other genera, the baculum of *Glyphotes* appears nearest to that of *Menetes*, but the lamina in this genus, although attached near the tip of the shaft, is very small and there are no discernible barbs.

The skull (Plates 7 (*a*), 7 (*b*), 8 (*a*)) is globular, with an exceptionally short, broad and deep rostrum. The junction of the nasals, premaxillae and maxillae forms an almost straight line joining the anterior edges of the anterior zygomatic roots. The nasals are short, broad and nearly parallel-sided, while the nasal aperture is flattened dorsally. The interorbital region is broad while the postorbital processes of the frontal are reduced and lie directly above the anterior edge of the posterior zygomatic root. The braincase is globular and not especially inflated. The orbit is more circular than in *Callosciurus* and is not placed especially far back, its anterior rim lying directly above p^4, with the lacrimal lying above p^4 and m^1. The zygomatic plate is weakly ridged and is slightly oblique, more vertical than in *Callosciurus*, its orbital edge ascending above the posterior face of p^4. The zygomatic arch is moderately strong with a small jugal process lying at the lowest part of the arch. The posterior zygomatic root is formed as in *Callosciurus*, the orbital surfaces of the alisphenoid and squamosal only slightly ridged and not forming a shelf as in *Nannosciurus*. The postorbital process of the jugal is rounded posteriorly as in *Callosciurus*. The anteorbital foramen is large, that part of the zygomatic plate lying over the infraorbital canal slightly reduced and narrow. The anterior palatine foramina are large and extend posteriorly to the maxillary suture. The palate is wide and terminates just beyond m^3, with no pronounced posterior palatal spicule. The maxillary tooth rows are parallel for much of their length but converge slightly posteriorly while the mesopterygoid fossa is moderate and the pterygoids not excessively developed. A narrow ectopterygoid is present. The bullae are not inflated. The mandible is weak with a minute coronoid process, lower in height than the condylar process, which itself is slender and much elongated posteriorly. The angular process is narrow and unthickened.

The incisors (Plate 8 (*b*)) are orthodont and very much specialized. The upper incisors are broadened but not thickened antero-posteriorly, their surfaces without grooves and with the anterior surface strongly convex. The outer lateral faces are strongly concave, the inner faces correspondingly convex so that for their terminal millimetre the teeth diverge from each other. The lower incisors are broadened, their anterior faces convex (not concave as stated by Thomas) and are not thickened antero-posteriorly. The lateral faces are similar to those of the upper incisors, the

teeth similarly divergent at the tips. The lower incisors are worn into broad, flat chisel-shaped blades, the inner corners more worn than the outer, so that viewed from the front the teeth present a shallow V-shape. That these peculiarities are not artifacts caused during skull cleaning is proved by their presence in the spirit specimen examined. The cheek teeth are of normal Callosciurine pattern with p^3 not especially reduced and the upper molars not excessively ridged. In the mandible, p_4 is slightly smaller than the lower molars and m_3 is not elongated, while the antero-internal cusps of the lower teeth are high as in *Callosciurus*.

The following measurements (in millimetres) are those of an adult male (B.M. 58.446) with measurements of the type specimen in parentheses : the skull of the Raffles Museum specimen is too fragmentary for measurement, but some measurements obtained from this skull and of Sarawak Museum 55.11 appear in Chasen & Kloss (1927). Total length of skull 29·1 (—), condylobasal length 25·9 (—), occipitonasal length 28·9 (—), basal length 23·5 (—), zygomatic breadth 19·0 (—), braincase breadth 16·4 (16·5), nasals, length × breadth 6·6 × 5·2 (6·7 × 5·3), diastema 6·0 (5·7), palatal length 13·2 (12·5), height of muzzle behind incisors 6·3 (6·1), breadth of muzzle over roots of incisors 7·5 (7·8), bulla, length × breadth 5·5 × 3·3 (5·0 × 3·0), maxillary tooth row 4·8 (4·8), $i^1 - i^1$ (tips) 3·4 (3·2), length × breadth p^3 0·7 × 1·1 (0·6 × 0·7), length × breadth p^4 1·0 × 1·2 (0·9 × 1·3), length × breadth m^1 1·1 × 1·3 (1·1 × 1·3), length × breadth m^2 1·1 × 1·4 (1·2 × 1·4), length × breadth m^3 1·0 × 1·2 (1·0 × 1·2), orbital length 9·6 (9·5), length from lacrimal notch to tip of nasals 10·5 (9·6).

Apart from its specialized incisors and greatly shortened muzzle, the skull of *Glyphotes* is similar to that of *Callosciurus notatus*, although, of course, much smaller. Certain cranial characters, however, such as the slight backward deflection of the components of the orbit, the obliquity of the zygomatic plate, which although more nearly vertical than in *Callosciurus* is more oblique than in *Nannosciurus*, the reduction of the postorbital processes and their backward displacement, the slight backward displacement of the lacrimal, a more circular orbitotemporal fossa and the reduction of the coronoid processes tend towards *Nannosciurus*, *Prosciurillus*, *Sciurillus* and *Myosciurus*. The structure of the baculum, the dentition and the major cranial characters, however, associate *Glyphotes* indubitably with *Callosciurus*.

The genus *Glyphotes* was placed by Ellerman (1940) in his " Lariscus " section of Sciuridae, a heterogeneous group containing *Lariscus*, *Menetes*, *Rheithrosciurus*, *Rhinosciurus* and *Hyosciurus* (an assemblage which Ellerman admits is not a natural group) the principal criterion being that these genera are much specialized and distinct from *Sciurus*. Simpson (1945), following Pocock (1923), places *Glyphotes* in the Callosciurini or Oriental tree squirrels. The cranial, dental and more especially the bacular characters of *Glyphotes* however, associate the genus more closely with *Callosciurus* than was thought by Ellerman and it seems best regarded as an offshoot of the ancestral stem of this widespread Oriental genus. The remarkable resemblance in colour pattern to *Callosciurus notatus* appears to be the result of parallelism : this pattern, with slight variation, reappears in *Callosciurus nigrovittatus*.

Widely divergent views exist on the classification of the dwarf Sciuridae of Borneo, Celebes, West Africa and South America. Earlier authors, i.e. Forsyth Major (1893), Thomas (1914, 1914*a*) and Miller & Gidley (1918) unite the dwarf squirrels in a subfamily, Nannosciurinae, based on certain dental and cranial characters common to each. A less extreme view is taken by Ellerman (1940) who places *Nannosciurus*, *Sciurillus* and *Myosciurus* in a *Nannosciurus* section of Sciuridae. By inference, the genus *Prosciurillus*, erected by Ellerman (1947) for *Sciurus murinus* Müller & Schlegel, would be placed in this section by Ellerman. Others, i.e. Pocock (1923) deny any close relation, mainly from the study of the penial characters, and suggest that similarities between these genera are the result of convergence, a view apparently adopted by Simpson (1945), who places *Nannosciurus* (and by inference *Prosciurillus*), *Sciurillus* and *Myosciurus* with the Callosciurini, Sciurini and Funambulini respectively. An important but limited contribution is made by Anthony & Tate (1935), who compare *Nannosciurus*, *Sciurillus* and *Sciurus* and conclude that a close relation must be presumed to exist between *Sciurillus* and *Nannosciurus*, despite differences in their bacula.

The skulls and bacula of *Callosciurus*, *Glyphotes*, *Microsciurus*, *Prosciurillus*, *Sciurillus*, *Myosciurus* and *Nannosciurus* have been compared, examining particularly those characters shared by the four latter, more extreme genera. Dental characters have not been taken into account: all but the last two genera have molars with the normal Sciurine ridge and depression pattern. Although suppressed in *Myosciurus* and *Nannosciurus*, as pointed out by Ellerman (1940) it is occasionally possible even so to trace the pattern in some skulls. Suppression of the pattern is much less evident in *Prosciurillus* and *Sciurillus*. Attention has been directed towards characters likely to be modified by the small size and specializations (when compared with *Callosciurus* or *Sciurus*) of the dwarf genera. The results are presented in Table I, itself extended and adapted from the tabular comparison of Anthony & Tate (1935).

Moore (1958) has extended *Prosciurillus* as defined by Ellerman (1947) to include *Callosciurus leucomus*, a species with a shortened orbit and which Ellerman (1940) points out is "almost transitional" to the *Nannosciurus-Sciurillus* type of skull. There is much to commend this action: *leucomus* differs considerably from *Callosciurus*, *sensu stricto*, in the form of its orbit, in the posterior displacement of its postorbital processes and in the obliquity of its zygomatic plate. Ellerman (1949), while including *leucomus* within *Callosciurus*, in fact suggested that it might warrant subgeneric rank within that genus. Moore, however, does not indicate that at the same time *leucomus* differs somewhat from *murinus*, the type species of *Prosciurillus*. It has well developed postorbital processes (like those of *Callosciurus*) which are not displaced posteriorly as far as those of *murinus*: its orbit, while less elongate than that of *Callosciurus* is less circular than that of *murinus*: good series of skulls of both forms show that the lacrimal is less extruded into the margin of the orbit than in *murinus*: the coronoid process is less reduced: the articulatory area of the jugal and squamosal is not reduced: the zygomatic plate is more oblique than in *murinus* and the posterior edge of the nasals is less advanced from a line joining the anterior zygomatic roots. It is clearly transitional between *Callosciurus*

and Nannosciurus

		Callosciurus notatus	*Glyphotes simus*	*Microsciurus similis*	*Microsciurus alfari*	*Prosciurillus leucomus*	*Prosciurillus murinus*	*Sciurillus pusillus*	*Myosciurus minutus*	*Nannosciurus melanotis*
1	Interorbital breadth / Length of frontal	0·82	0·93	0·79	0·81	0·85	0·81	1·00	0·96	0·87
2	Ectopterygoids	Slightly developed	Slightly developed	Very slight ridge	Very slight ridge	Well developed	Well developed	Well developed	None	Well developed.
3	Form of the orbitotemporal fossa	Elongate-oval	Less elongate, more circular	Similar to *G. simus* but more elongate	As in *G. simus* but more circular	Less elongate, more circular than *G. simus*	Almost circular, only slightly elongate	Circular	Circular	Circular.
4	Posterior displacement of postorbital process	None: lies above posterior face of m^3	Slight: lies above anterior face of the posterior zygomatic root	Slightly more posterior than in *G. simus*	As in *M. similis*	Slight: much as in *G. simus* but slightly more posterior	More posterior than in *G. simus:* lies above centre of posterior zygomatic root	As in *P. murinus*	Displaced to rear of orbit: above rear of posterior zygomatic root	As in *M. minutus.*
5	Postorbital process	Well developed	Much reduced	Reduced	Reduced	Well developed	Reduced	Much reduced	Minute	Minute.
6	Posterior edge of suborbit	Posterior to postorbital process	Just posterior to postorbital process	As in *G. simus*	Directly below base of postorbital process	Just posterior to or beneath tip of postorbital process	Anterior to postorbital process	As in *P. murinus*	As in *P. murinus*	As in *P. murinus.*
7	Position of suborbit	Posterior to orbit	Extends to orbit	,,	As in *G. simus*	As in *G. simus*	As in *G. simus*	As in *G. simus*	As in *G. simus*	As in *G. simus*
8	Separation of frontal process of premaxilla from lacrimal by the maxillary-frontal suture	Moderate	As in *C. notatus*	As in *C. notatus*	As in *C. notatus*	More widely separated than in *C. notatus*	As in *P. leucomus*	As in *P. leucomus*	Wide separation	Wide separation.
9	Position of lacrimal	Mainly withdrawn from orbit: between frontal and zymatic process of maxilla	As in *C. notatus*, but slightly extruded into orbital margin	,,	,,	As in *C. notatus*	Slightly extruded into orbital margin	More extruded	Extruded into orbital margin	Almost wholly extruded into orbital margin.
10	Upper incisors	Slightly prodont	Orthodont	Slightly prodont	Proodont	Proodont	Proodont	Strongly prodont	Strongly prodont	Strongly prodont.
11	Area of maxilla representing infraorbital part of masseter	Considerably less than area of region of premaxilla just anterior	As in *C. notatus*	Less than premaxillary area	As in *M. similis*	As in *M. similis*	About equal to premaxillary area	Slightly greater than premaxillary area	As in *C. notatus*	Greater than premaxillary area.
12	Presence of flange or ridge on orbital surface of alisphenoid from base of squamosal to origin of external pterygoid muscle	None or only slight	Very slight ridge	Incipient	Incipient	Very slight ridge	Incipient	Pronounced ridge	Pronounced ridge	Pronounced ridge.
13	Inflation of alisphenoid just anterior to bulla	None	Incipient	,,	,,	Incipient	Slight	Inflated	Inflated	Inflated.
14	Coronoid process	Normal	Much reduced: minute	Much reduced: minute	Reduced	Slightly reduced	Much reduced	Much reduced: minute	Obsolescent	Obsolescent.
15	Condylar process	,,	Slender: very elongate, hooked	Normal: slightly hooked	Slightly elongate: hooked	Slightly elongate: hooked	Elongate: hooked	Slender: elongate, hooked	As in *S. pusillus*	As in *S. pusillus.*
16	Posterior edge of nasals	Lie on a line joining anterior edges of orbits	As in *C. notatus*	Slightly anterior to this line	As in *M. similis*	As in *M. similis*	In advance of this line	As in *P. murinus*	Well in advance of this line	As in *M. minutus.*
17	Posterior palatal spine	Present	Minute	Absent	Absent	Present	Absent	Minute	Absent	Minute.
18	Insertion of internal pterygoid muscle	Not deep	Deeper than in *C. notatus*	Moderate	Deep	As in *G. simus*	Deep	Deep	Shallower than *P. murinus*	As in *M. minutus.*
19	Postorbital process of jugal	Present, flattened	Present, well developed	Present, well developed	Present, well developed	Present, well developed	Present, well developed	Absent	Present well developed	Present, well developed.
20	Articulation of jugal with squamosal	Broad jugal with extensive articulatory area	As in *C. notatus*	As in *C. notatus*	As in *C. notatus*	As in *C. notatus*	Articulatory area slightly reducd	Jugal slender, extensive articulatory area	As in *S. pusillus*	Jugal broad, articulatory area reduced.
21	Obliquity of zygomatic plate	Sharply oblique	Less oblique than in *C. notatus*	Slightly less oblique than *C. notatus*	As in *G. simus*	As in *M. similis*	As in *G. simus*	Nearly vertical	Vertical	Vertical.
22	Baculum	Slender shaft with blade-like lamina	As in *C. notatus*	Not seen	Not seen	Not seen	Not seen	Straight shaft with upturned spatulate tip	Straight shaft with thickened base and tip	Hinged, hook shaped shaft with lamina.

and *Prosciurillus murinus* and since its differences from the latter species are mainly small differences of degree it seems best included in that genus as defined by Moore. Furthermore, *Prosciurillus abstrusus*, described as new by Moore (1958) seems from the description to be intermediate in some respects between *murinus* and *leucomus*. *Microsciurus* has been included in Table I since, like *Prosciurillus*, it is a transitional genus between the true dwarf squirrels and the larger *Callosciurus* and *Sciurus*. *Microsciurus similis*, transferred to *Sciurillus* by Ellerman (1949), is considerably less specialized than that genus and for the purposes of the present paper is retained within *Microsciurus*.

Gradual divergence from the normal condition exemplified by *Callosciurus notatus* appears in a number of characters. Some of the characters examined are at least in part the direct result of the shortening of the base of the skull and its arcuate deflection. Such characters are the circular form of the orbit, the rearward displacement of the postorbital process, the separation of the frontal process of the premaxilla from the lacrimal by a projection of the maxilla, the extrusion of the lacrimal into the orbital margin, the forward extension of the suborbit, a tendency for the incisors to become strongly proodont, a lessening of the obliquity of the zygomatic plate and alterations in the form of the nasals. Others appear related to this cause less for mechanical reasons but through alterations in muscle attachments i.e. the development of alisphenoid ridges, increases in the relative area of the maxillary insertion of the masseter and alterations in the articulatory parts of the mandible. Yet others appear adventitious, such as the presence or absence of a post-palatal spine, the form of the jugal process and the presence or absence and degree of development of the ectopterygoids.

Sciurillus, *Myosciurus* and *Nannosciurus* are seen to be the most extreme genera. Of these, *Myosciurus* and *Nannosciurus*, the smallest genera, are the most divergent. *Sciurillus* occupies a position intermediate between *Microsciurus*, *Prosciurillus* and the extreme genera. *Myosciurus* and *Sciurillus* are further specialized in the form of the zygomatic plate, which in *Myosciurus* is greatly reduced and in *Sciurillus* is grooved above the anteorbital foramen. This aperture in *Prosciurillus*, *Sciurillus* and *Nannosciurus* lies well in advance of the anterior end of the maxillary tooth row. *Prosciurillus* and *Microsciurus* are transitional between *Glyphotes* and the more extreme genera and display many of their characters in lesser degree. The skull of *Microsciurus* closely resembles that of *Prosciurillus*, both genera displaying the characters considered here at about the same level of development. This factor no doubt led Ellerman (1940) to associate *Prosciurillus murinus* with *Sciurillus* and later (1949) to transfer *Microsciurus similis* to *Sciurillus*. Both genera, however, are less specialized than *Sciurillus*: *Microsciurus similis* (transitional to *Sciurus*) in fact stands further from *Sciurillus pusillus* than does *Prosciurillus leucomus* (transitional to *Callosciurus*) to *Prosciurillus murinus*. *Glyphotes* connects *Prosciurillus* and *Callosciurus* in the development of its skull while *Microsciurus*, considerably more advanced in the development of the characters considered, provides a more remote link between *Sciurillus* and *Sciurus*. Such bacula as have been examined suggest no relation between the genera. That of *Glyphotes* is typically Callosciurine, while the baculum of *Sciurillus* is said by

Anthony & Tate (1935) to resemble that of *Sciurus* (*Sciurus niger*). The baculum of *Myosciurus*, which stands somewhat apart from other Sciurid bacula, resembles most closely in its small size and terminally thickened rod-like form the bacula of the African tree squirrels. The hook-shaped, laminated baculum of *Nannosciurus* is nearest to the " Tomeutes " type of Thomas (1915). No regular pattern is displayed by the adventitious characters. The form of the postorbital process of the jugal is variable, but its position on the arch of the zygoma appears related to the shortening of the orbit. It is on or near the lowest part of the arch in *Callosciurus*, *Glyphotes*, *Microsciurus* and *Prosciurillus*. In *Myosciurus* and *Nannosciurus* it is pushed forward to a position on the anterior ascending part of the arch, while *Sciurillus* displays an intermediate condition.

There appears to be no intermediate genus comparable with *Glyphotes* or *Microsciurus* among the African tree squirrels. Reduction of size and relative shortening of the rostrum, however, occur within the genus *Paraxerus*, of which the smaller members, on account of certain external and dental characters, are usually considered a subgenus, *Tamiscus*. The larger species of *Paraxerus* (the *cepapi*, *flavivittis* and *palliatus* groups of Ellerman (1940)) have skulls similar to *Callosciurus* in many respects and show no trace of the specializations of dwarf genera. Some of these characters appear among the members of the subgenus *Tamiscus*, all of which are smaller and have a relatively shorter rostrum. The orbitotemporal fossa is shortened and less elongated than in the larger species and the postorbital processes are displaced posteriorly to lie slightly in advance of (*boehmi*, *emini*, *vulcanorum*, *antoniae*) or above (*alexandri*) the anterior face of the posterior zygomatic root. There is a very slight ridge on the alisphenoid and the upper incisors are more proodont than in the larger species. The mandible, however, has remained unspecialized and there is no lessening of the obliquity of the zygomatic plate.

The grouping of the Celebean genus *Prosciurillus*, the South American genus *Sciurillus*, the West African genus *Myosciurus* and the Bornean genus *Nannosciurus* in one subfamily is unconvincing on zoogeographical grounds. All are highly specialized genera, widely divergent from *Sciurus* or *Callosciurus*, sharing in common a number of cranial characters which appear mostly to be related to the common factor of greatly reduced size. *Prosciurillus*, the largest, is a " giant " among these pygmy genera, and is the least divergent from *Callosciurus*. They diverge considerably among themselves. *Myosciurus* is particularly aberrant, and so far as comparison has been possible, their bacula have been found to differ widely, usually resembling in each case the bacula of the more normal tree squirrels of the region in which the dwarf is found. Study of the " semi-dwarf " *Glyphotes*, *Microsciurus* and *Prosciurillus* reveals that the characters appearing in extreme form among the most divergent genera are found in them in lesser degree and that these intermediate genera connect the " Nannosciurinae " to *Callosciurus* and *Sciurus*. The characters show difference in degree within the genus: *Prosciurillus murinus* ranks closely to the more extreme *Sciurillus* but the larger *Prosciurillus leucomus* displays considerable affinity with *Callosciurus* and, in the absence of the smaller species, would possibly warrant subgeneric rank within *Callosciurus*. The evidence therefore

suggests that rather than forming a unit with biological reality, the dwarf squirrels of Celebes, Borneo, West Africa and South America have evolved independently. The grouping by Simpson (1945) of these squirrels with the tree squirrels of their respective regions appears a more accurate representation of their relationships than placing them in an artificial group which ignores the genera connecting them to the other members of the Sciuridae.

REFERENCES

Banks, E. 1931. A popular account of the mammals of Borneo. *J. Malay Br. Roy. As. Soc.* **9**, 2 : 1–139, pls. 11–19, map.

Chasen, F. N. & Kloss, C. B. 1927. A rare Bornean Squirrel, *Glyphotes simus* Thomas. *Ibid.* **5** : 349–350.

Didier, R. 1952. Etude systématique de l'os pénien des mammifères. Rongeurs. *Mammalia*, **16** : 7–23.

Ellerman, J. R. 1940. *The Families and Genera of Living Rodents.* Vol. 1. London : British Museum (Natural History).

—— 1947. Notes on some Asiatic Rodents in the British Museum. *Proc. zool. Soc. Lond.* **117** : 259–271.

—— 1949. *The Families and Genera of Living Rodents.* Vol. 3, pt. 1. London : British Museum (Natural History).

Forsyth-Major, C. J. 1893. On some Miocene squirrels, with remarks on the dentition and classification of the Sciuridae. *Proc. zool. Soc. Lond.* 179–215, pls. 8–11.

Miller, G. S. & Gidley, J. W. 1918. Synopsis of the supergeneric groups of Rodents. *J. Wash. Acad. Sci.* **8** : 431–448.

Moore, J. C. 1958. A new species and a redefinition of the squirrel Genus *Prosciurillus* of Celebes. *Amer. Mus. Novit.* No. 1890 : 1–5.

Pocock, R. I. 1923. The classification of the Sciuridae. *Proc. zool. Soc. Lond.* 209–246, figs. 18–29.

Simpson, G. G. 1945. The Principles of classification and a classification of Mammals. *Bull. Amer. Mus. nat. Hist.* **85** : i–xvi, 1–350.

Thomas, O. 1914. *Proc. zool. Soc. Lond. Abstract.* No. 133 : 36.

—— 1914*a*. On a remarkable case of affinity between animals inhabiting Guiana, West Africa, and the Malay Archipelago. *Proc. zool. Soc. Lond.* 415–417.

—— 1915. The penis-bone, or " Baculum ", as a guide to the classification of certain squirrels. *Ann. Mag. nat. Hist.* **15** : 383–387.

PLATE 7

(*a*) *Glyphotes simus.* Dorsal aspect skull and ventral aspect mandible. × 3·5.
(*b*) *Glyphotes simus.* Ventral aspect skull and dorsal aspect mandible. × 3·5.

PLATE 8

(*a*) *Glyphotes simus.* Lateral aspect skull and mandible. × 2·5.
(*b*) *Glyphotes simus.* Frontal aspect incisor teeth. × 3.
(*c*) *Glyphotes simus.* Dorsal aspect baculum. × 5.
(*d*) *Glyphotes simus.* Lateral aspect baculum. × 5.
(*e*) *Glyphotes simus.* Dorsal aspect tip of baculum. × 12.
(*f*) *Glyphotes simus.* Lateral aspect tip of baculum. × 12.